

Ground beetle community responses to heavy metal contamination

Tomasz Skalski, David Stone, Paulina Kramarz, Ryszard Laskowski

Skalski T., Stone D., Kramarz P., Laskowski R. 2010. Ground beetle community responses to heavy metal contamination. *Baltic J. Coleopterol.*, 10(1): 1 – 12.

The effects of chronic heavy metal contamination on ground beetle community structure were investigated at five sites located along a pollution gradient caused by zinc-and-lead industry in southern Poland. Concentrations of Zn, the main pollutant, in humus layer along the gradient ranged from ca. 150 mg kg⁻¹ at the reference site (32 km from the pollution source) to 10500 mg kg⁻¹ at the most polluted site. The general species composition, as analyzed by Principal Components Analysis, did not show clear differences between sites that may be linked directly to the pollution level. Instead, soil habitat moisture was found as an important factor for species composition. However, species abundance and richness decreased significantly with increasing pollution level. Although species diversity (McIntosh index) also generally decreased with increasing metal concentration, the trend was not clear compared with the trends for abundance and richness. We hypothesize that this may be caused by site-specific interspecies competition and niche overlap. Autumn-breeders appeared more sensitive to pollution compared with spring-breeders. We assume that this may be caused by differences in life-history patterns, with spring-breeders characterized by short larval stage and a relatively long adult life throughout the growing season that is more resistant to metal pollution.

Key words: Carabidae, community structure responses, heavy metals, chronic pollution

Tomasz Skalski. Department of Entomology, Jagiellonian University, Ingardena 6, 30-060 Kraków, Poland

David Stone. Oregon Department of Human Services, 800 NE Oregon St., Portland, OR 97232, USA

Paulina Kramarz, Ryszard Laskowski. Department of Ecotoxicology, Jagiellonian University, Gronostajowa 3, 30-387 Kraków, Poland

INTRODUCTION

Different factors and processes may cause extinctions of natural populations of animals and plants. In industrialized regions the exposure to pollutants released by human activity seems to be a principal cause (Hopkin & Martin 1984, Laskowski & Hopkin 1996, Hakoyama et al. 2000). Single-species or two-species studies dominate

ecotoxicological research, since elucidation of mechanisms at higher levels of ecological organization is extremely difficult. However, species-by-species studies provide no information about responses to heavy metal contamination occurring at the community level. Carabid beetles are widely known as good indicators of environmental changes (Thiele 1977, Dritchilo & Ervin 1982, Desender et al. 1994, Eyre

et al. 1996) However, there is still scant information on potential effects of chronic pollution on the structure of carabid beetle communities. High metal concentrations usually decrease the survival probability (Sousa 1984). For example, Mozdzer et al. (2003) found significantly increased mortality of *Pterostichus oblongopunctatus* larvae fed zinc or cadmium contaminated food. Other effects observed in ground beetles exposed to metal contamination included decreased fecundity, decreased body mass and/or increased development time (Kramarz 2000). All these effects may result in decreased abundance of ground beetles in metal polluted environments (Freitag et al. 1973, Gongalskii and Butovsky 1997). On the other hand, Read et al. (1987) did not find significant effect of increasing heavy metal pollution on carabid abundance or species diversity.

Anthropogenic contamination is one of a number of possible disturbances in ecosystems. As such, it can be useful for testing more general ecological hypotheses on relation between species richness, diversity and level of disturbance. An interesting case was reported by Connell (1978) who demonstrated that coral reef communities were more diversified at intermediate level of disturbances (on the scale of frequency and intensity). Inconsistencies in results of studies on the effects of pollution on species diversity may be explained by Connell's (1978) intermediate disturbance hypothesis. According to this hypothesis, most diverse communities occur at intermediate levels of disturbances (on the scale of frequency and intensity).

The scope of this study was to examine the influence of a chronic disturbance (metal pollution) at different levels of intensity (metal concentrations) on the diversity and abundance patterns in ground beetle communities. The studies were conducted during the spring, when both spring and autumn breeding species occur simultaneously.

MATERIALS AND METHODS

Samples of carabid beetles were collected in high season recommended as the most efficient (Duelli et al 1999) from May to June in the Olkusz region of southern Poland, near zinc-and-lead mines and smelters. A 31-km long transect was established with five sampling plots differing in their levels of pollution (Table 1). All plots were located in one relatively unfragmented Scots pine forest complex (*Pino-Quercetum* type), which is the most common forest formation in Poland (Szafer et al. 1976) (fig. 1). Fifty Barber-type live traps (plastic cups 10 cm diameter, 15 cm deep) were placed at each plot in two rows, about 5 m apart from each other. The traps were emptied every third day, and the trapped carabids were brought to the laboratory and killed by freezing. The beetles were then identified to species level and all representatives of a species were counted.

Statistical analysis

To detect patterns in species composition of the carabid community, the Principal Components Analysis on standardised species-sample matrices was used. Species abundance were $\log(N+1)$ transformed to improve normality of the distributions.

The following data were analysed for each site: relative abundance of carabids (N), species richness and McIntosh diversity indices (Magurran 1988). Additionally, rank abundance curves and slopes of linear regression equations of abundance rank were plotted (May 1975). The significance of contrasts between localities was determined by the Wilcoxon signed matched pairs test. To compare the magnitude of interspecific competition in a community, species niche overlap indices (\hat{a}) (Pianka 1974) were calculated for each site. The niche relations among carabids were illustrated with a dendrogram, using relative Euclidean distance procedure. Two-tailed Spearman rank-correlation coefficient was adopted to investigate relationships between characteristic metrics of a community structure, population abundance of dominant species and

Table 1. Concentrations of major pollutants in humus layer at the study sites; SD - standard deviation

Site	Distance from the smelter*	Zn [mg kg ⁻¹]		Cd [mg kg ⁻¹]		Cu [mg kg ⁻¹]		Pb [mg kg ⁻¹]	
	[km]	average	SD	average	SD	average	SD	average	SD
1**	3.5	10454	2618.5	81.92	17.72	46.9	4.56	2635	120.4
2	2.5	5104	729.0	51.06	19.34	37.6	3.72	1832	215.0
3	3.9	1522	135.2	18.14	2.60	25.6	2.16	870	36.3
4	7.9	244	78.2	3.30	1.03	15.4	2.68	355	30.9
5	31.9	151	34.5	0.84	0.39	10.7	0.96	136	8.8

* Distance from the larger of the two smelters is given.

** Site 1 is actually located between the two smelters, hence the contamination is higher than at OLK3 despite somewhat larger distance from the larger smelter.

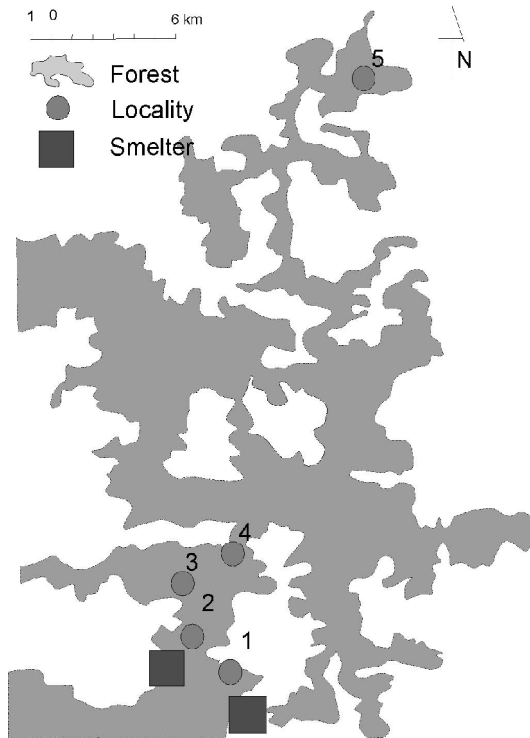


Fig. 1. Map of the Olkusz smelter vicinity, showing current forest cover and study sites

environmental metrics (heavy metal concentrations and distance from the smelter).

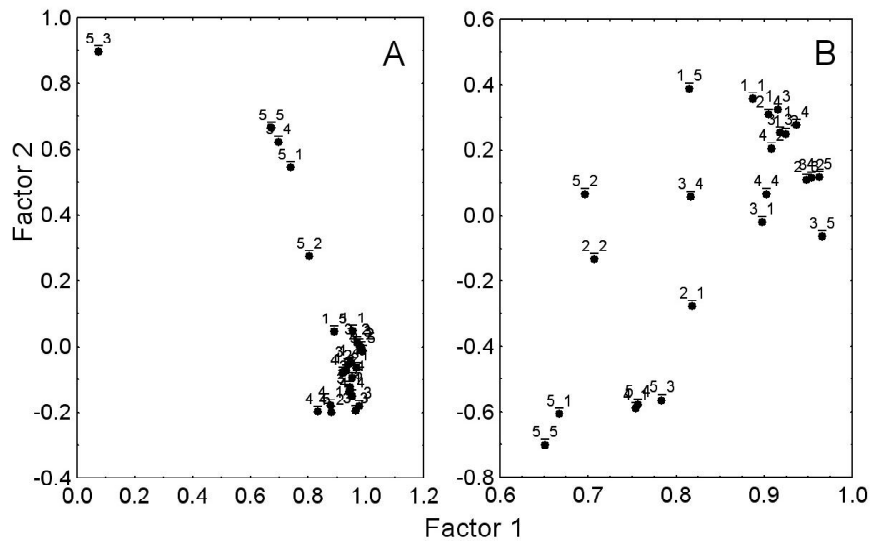
RESULTS

A total of 3300 carabids representing 24 different species were collected (Table 2). All species which were abundant were also frequent, suggesting that their abundance reflects their position in a community on each locality. Five species obtained from the reference site were absent on polluted sites (*Carabus auronitens*, *C. glabratus*, *C. hortensis*, *Abax carinatus*, *A. ovalis*). Five other species, *C. arvensis*, *C. nemoralis*, *C. violaceus*, *Pterostichus niger* and *P. oblongopunctatus*, were common at most sites. The remaining 14 species were present at low frequency and abundance.

The Principal Components Analysis for the May sample summarised 79.3% and 9.1% of the total variance for the first and second axis respectively (fig. 2A). A biplot of the location of the samples suggests that two clear clusters were formed. The first was created by all localities up to 10 km away from the factory. The second one was formed by samples from the reference site (30 kilometres from the pollution source), but their dispersion tended to join the rest of the samples. Closer inspection of the factor pattern for these axes

Table 2. Frequency and abundance of ground beetles on investigated localities; B.m. – breeding mode: sb = spring breeders, ab = autumn breeders

Species	B.m.	Frequency (%)					Abundance (n)					Total number of specimen
		Locality					Locality					
		5	4	3	2	1	5	4	3	2	1	
<i>Carabus arcensis</i> Herbst	sb	11	10	10	10	9	137	56	42	210	99	544
<i>Carabus auronitens</i> Fabr.	sb	11	0	0	0	0	32	0	0	0	0	32
<i>Carabus convexus</i> Fabr.	sb	1	0	0	0	0	1	0	0	0	0	1
<i>C. glabratus</i> Payk.	ab	10	0	0	0	0	165	0	0	0	0	165
<i>C. hortensis</i> L.	ab	6	0	0	0	0	11	0	0	0	0	11
<i>C. nemoralis</i> Mull.	sb	6	8	2	7	1	19	26	4	10	1	60
<i>C. violaceus</i> L.	ab	9	7	4	0	2	170	26	12	0	6	214
<i>Leistus rufescens</i> (Fabr.)	ab	0	1	0	0	0	0	1	0	0	0	1
<i>Nebria brevicollis</i> (Fabr.)	ab	0	0	0	0	1	0	0	0	0	1	1
<i>Notiophilus biguttatus</i> (Fabr.)	sb	0	6	0	0	2	0	10	0	0	2	12
<i>Bembidion lampros</i> (Herbst.)	sb	0	1	0	0	0	0	1	0	0	0	1
<i>Amara curta</i> Dej.	sb	0	1	0	0	0	0	1	0	0	0	1
<i>Pterostichus nigrita</i> (Payk.)	sb	1	0	0	0	0	1	0	0	0	0	1
<i>P. caerulescens</i> (L.)	sb	0	4	0	0	0	0	4	0	0	0	4
<i>P. cupreus</i> (L.)	sb	0	2	0	0	0	0	3	0	0	0	3
<i>P. niger</i> (Schall.)	ab	5	7	4	3	1	20	20	11	9	1	61
<i>P. oblongopunctatus</i> (Fabr.)	sb	11	10	11	10	10	632	356	148	573	245	1954
<i>P. strenuus</i> (Panz.)	sb	0	0	0	0	1	0	0	0	0	1	1
<i>P. vulgaris</i> (L.)	ab	1	0	0	1	0	1	0	0	1	0	2
<i>Abax carinatus</i> (Duft.)	ab	10	0	0	0	0	57	0	0	0	0	57
<i>A. ovalis</i> (Duft.)	ab	11	0	0	0	0	127	0	0	0	0	127
<i>Calathus melanocephalus</i> (L.)	ab	2	1	0	1	2	2	2	0	1	3	8
<i>Agonum muelleri</i> (Herbst)	sb	0	1	0	0	0	0	1	0	0	0	1
<i>Harpalus latus</i> (L.)	ab	4	0	0	4	3	6	0	0	7	3	16

Fig. 2. Principal Component Analysis for the May (A) and June (B) samples on $\log(N+1)$ abundances of total faunas in each sampling week (X_y – sample y in locality X).

revealed that the second axis was principally related to the occurrence of moisture preferring species such as *C. glabratus* and *A. ovalis* (loadings of 1.33, 1.43). The highest loadings on the first axis were assigned to *C. arvensis* and *P. oblongopunctatus* (loadings 1.3, 2.5).

as one assemblage. However, some species (e.g. *C. glabratus*, *C. auronitens*, *A. carinatus*, *A. ovalis*) were limited to the reference site only. All of them are moisture-preferring species and their limitation to the reference site may reflect strict

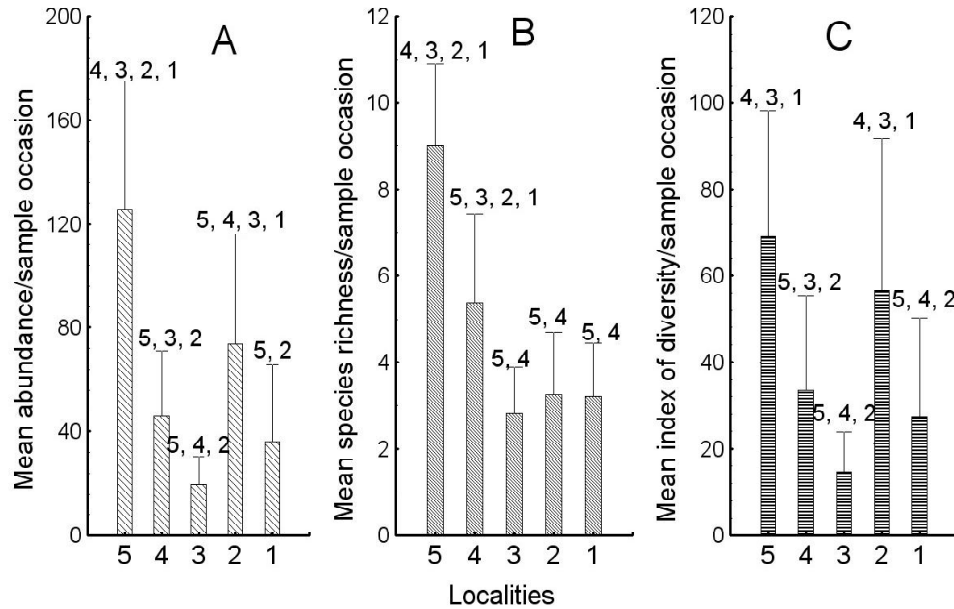


Fig. 3. Mean (+SD) community structure parameters on each locality (1-5). Significant differences for means are marked above each graph (Wilcoxon matched pair test, $p < 0.05$).

The equivalent analysis for the June samples summarised 73.7% and 10.5% of the total variance on the first and second axis respectively (fig. 2B). Although no clear clusters were formed, the main division between the reference site and the rest of the localities is visible. In that month, the highest loadings on the first axis were found for *C. arvensis* and *P. oblongopunctatus* (1.3, 2.7), and on the second axis – for *C. glabratus*, *C. violaceus* and *C. nemoralis* (-1.53, -2.04, 0.92 respectively).

Comparing overall results, no evident differences in species composition between localities were found at this stage of data analysis. The lack of clear differences between localities may reflect specimen exchange between the study sites during May and June and suggests treating them

Table 3. Spaermann rank-correlation coefficients (R) and their significance levels (p) for community and population parameters along zinc concentration gradient (correlations with other metals were the same due to strict correlation between metal concentrations along the pollution gradient)

	R	p
Assemblage parameters		
Abundance	-0.60	0.0001
Richness	-0.70	0.0001
Diversity	-0.33	0.05
Population abundance		
<i>Carabus arvensis</i>	0.02	0.86
<i>Carabus nemoralis</i>	-0.34	0.01
<i>Carabus violaceus</i>	-0.62	0.0001
<i>Pterostichus oblongopunctatus</i>	-0.25	0.07
<i>Pterostichus niger</i>	-0.34	0.01

environmental requirements, not connected to pollution levels.

To establish possible links between ordination scores of the samples, the Spearman-Rank correlation analyses were carried out with respect to main community variables and concentrations of major pollutants in humus layer. All community indices were negatively correlated with pollution level expressed as metal concentrations (Table 3). Despite this tendency, there were no

statistically significant differences between some localities (Wilcoxon test). Figure 3A shows no significant difference in species relative abundance between two pairs of localities: 4-1 and 3-1. No differences in species richness were observed between sites 1, 2 and 3 (fig. 3B). Surprisingly, no difference in species diversity was observed between the site pairs: 5-2, 4-1 and 3-1 (fig. 3C). Mean scores of diversity index on locality 2 were even higher than on locality 4 and 3.

Table 4. Spatio-temporal niche overlap for the most abundant species

Species		1	2	3	4	5	6	7	8	9	10
<i>Carabus arvensis</i>	1	1.00	0.18	0.18	0.17	0.36	0.25	0.70	0.20	0.16	0.16
<i>C. auronitens</i>	2	0.18	1.00	0.58	0.47	0.18	0.35	0.30	0.04	0.63	0.63
<i>C. glabratus</i>	3	0.18	0.58	1.00	0.80	0.10	0.66	0.21	0.11	0.75	0.75
<i>C. hortensis</i>	4	0.17	0.47	0.80	1.00	0.14	0.50	0.10	0.04	0.54	0.54
<i>C. nemoralis</i>	5	0.36	0.18	0.10	0.14	1.00	0.16	0.41	0.07	0.13	0.13
<i>C. violaceus</i>	6	0.25	0.35	0.66	0.50	0.16	1.00	0.38	0.44	0.55	0.55
<i>Pterostichus oblongopunctatus</i>	7	0.70	0.30	0.21	0.10	0.41	0.38	1.00	0.28	0.28	0.28
<i>P. niger</i>	8	0.20	0.04	0.11	0.04	0.07	0.44	0.28	1.00	0.10	0.10
<i>Abax carinatus</i>	9	0.16	0.63	0.75	0.54	0.13	0.55	0.28	0.10	1.00	0.79
<i>A. ovalis</i>	10	0.16	0.63	0.75	0.54	0.13	0.55	0.28	0.10	0.79	1.00
Mean niche overlap		0.33	0.44	0.51	0.43	0.27	0.48	0.39	0.24	0.49	0.49

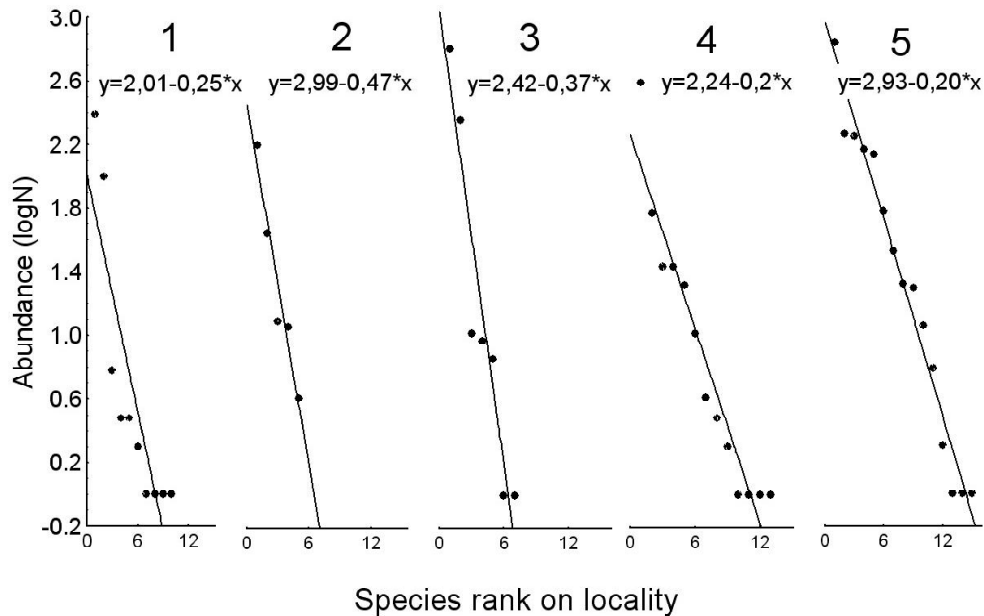


Fig. 4. Rank-abundance curves (log scale) with linear regressions for the five investigated assemblages (1-5)

The curves of species abundance against species rank illustrate the evenness component of diversity (fig. 4). The analysis of pooled material indicates a close fit of all curves to the geometric series (Kolmogorow-Smirnoff, $p < 0.01$). The slopes of the linear regression lines rank the pollution effect on the community structure in the same order as the McIntosh diversity index does. Additionally, the shallower slope for the reference site in comparison to the polluted sites, which has a more sigmoid shape, indicates more available resources at the reference site.

Responses of particular dominant species to environmental variables differed. Relative abundance of *C. violaceus*, *C. nemoralis* and *P. niger* decreased with increasing pollution level (Table 3). No such significant effect was found for *C. arvensis* and *P. oblongopunctatus*.

Table 4 shows a spatio-temporal niche overlap for those species whose dominance exceeded 1% in the whole community. *C. arvensis* and *P. oblongopunctatus* (the two most abundant species), exhibit very low mean niche overlap ($\alpha = 0.33$). This indicates that the species are poor competitors, avoiding coexistence with other species. The highest values of niche overlap calculated for reference site species, may indicate higher availability of resources on that site. In order to gain some idea of the characteristics

involved in table 4, cluster analysis was applied. The results showed two distinct groups of species in the dendrogram (fig. 5). The first one is created by species occurring only at the reference site and *C. violaceus*. All remaining species, occurring along the whole pollution gradient, are placed in the second cluster. High scores for the Euclidean distance between *C. violaceus* and the rest of the widely distributed species, indicates strong competition relations.

DISCUSSION

Many papers have been put forward to criticize pitfall trapping methodology in studies of community abundance and structure. The major disadvantage of pitfall traps is that the collection rate reflects population density as much as animal activity (Greenslade 1964, Luff 1975, Thomas et al. 1998). Abundance on each site is affected by temperature and plant cover (Honek 1997 a, b). In the present study, the vegetation structure of the sampling sites was fairly uniform, with an exception of site 1, where pine forest was visibly affected by pollution, resulting in smaller tree heights and almost no ground cover. The traps on all sites were emptied the same day, so fluctuations in weather were minimized. Moreover, the study was restricted to ground beetle communities only, thus the relation

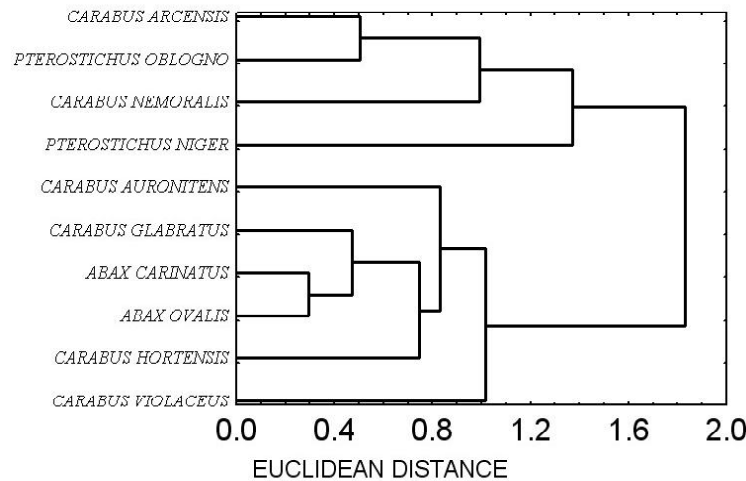


Fig. 5. The niche overlap dendrogram of the ten the most abundant species

between activity and abundance should be satisfactory and the same for all sites. As a result of these factors, we believe that our sampling is representative of the community structure at all sites.

Although we found significant reduction of community abundance with increasing metal concentration, this result cannot be conclusively interpreted as a direct effect of pollution. A general constraint with studies that relate population density or community structure to contamination level along pollution gradients is the fact that metal pollution usually causes extensive changes in ecosystem function. For example, litter decomposition is retarded by heavy metals (e.g., Berg et al. 1991, Niklińska et al. 1998), resulting in accumulation of large amounts of undecomposed dead organic matter on the forest floor (e.g., Coughtrey et al. 1979, Grodziński et al. 1990). This, in turn, changes the habitat of soil-dwelling and epigeic species. Such changes in organic matter quality and possible direct effects of contaminants on ground beetle populations and communities are expected to go in parallel along pollution gradients, thus making the distinction. Nevertheless, from the perspective of population persistence and community structure in polluted sites, such a distinction is not the primary goal in our opinion. The fundamental question that studies of this nature have to answer is whether pollution results in important alterations in the structure of communities inhabiting contaminated areas.

With this in mind, we tried to separate direct and indirect effects with through closer examination of the available data. One noticeable gradient accompanying the metal pollution is accumulation of organic matter and soil moisture, with the most polluted sites having the thickest and driest soil organic layer. This trend is likely responsible for the occurrence of the five moisture preferring species at the reference site only (*Carabus auronitens*, *C. glabratus*, *C. hortensis*, *Abax carinatus*, *A. ovalis*). However, if the moisture gradient was the main factor controlling the ground beetles communities, then species which prefer more dry habitats, such as *C.*

nemoralis, *C. violaceus* and *P. niger* (Eyre 1994), would be more abundant at drier and more contaminated sites. This was not the case in our studies, and all these species were also present in much higher abundances at the reference site compared with the contaminated ones. Also another species preferring dry soils, *C. arvensis*, (Eyre 1994), should be significantly more abundant on more dry sites but no such trend was found.

Another factor, which could reduce abundance in the community, is a decrease in the spectrum of available resources. The main sources of food for carabid beetles are earthworms and springtails (Thiele 1977, Hengeveld 1980 ab, b, c), the groups whose biomass usually decreases with increasing metal pollution (Strojan 1978). In fact, Read et al. (1987) observed that obligatory diapause, which is controlled by fat reserves, was disrupted due to starvation in populations of *Nebria brevicollis* inhabiting polluted areas. Taking into account that ground beetles are poor accumulators of metals (Gongalski and Butovsky, 1997), starvation and perhaps increased competition for limited food resources, could be the major reasons for decreased population densities and species richness at the most polluted sites.

Our results indicate that species that breed in the spring were less sensitive to pollution compared with autumn-breeders. In contrast, Read et al. (1987) found that autumn breeders were more abundant in contaminated sites. However, may have been due to the occurrence of a particular autumn breeding species, *N. brevicollis*, with the ability to prolong its life cycle, at high densities. Why were autumn breeders such as *C. violaceus* and *P. niger* significantly more affected by the pollution than spring breeders in our study? The main difference between the two groups is their mean generation life span, which is shorter for the spring breeders. However, the life span of adults is longer in spring breeding species, whereas life span of larva is extremely short. According to Grüm (1975), the active stages from eggs until pupae suffer highest mortality in carabid beetles. This may be of

particular importance in polluted environments as ground beetle larvae can be more sensitive to toxic chemicals in soil simply due to their life history characteristics (more direct contact with soil solution) and thinner external cuticle barrier. Also, as Rayms-Keller et al. (1998) observed on mosquitos, their larval stage was particularly vulnerable to metal toxicity due to metal-caused developmental anomalies. Thus, the shorter the time of the larval stage, the higher the reproductive success. Prolonged time of the adult instar can also result in greater opportunity to secure a better food supply, which is necessary for high fecundity (Walin et al. 1992). As Chaabane et al. (1994) mentioned, during the first three months of adult life, dry weight production of *Abax ater* was almost twice the production during the seven months of larva life. All these data suggest that spring breeders should be more resistant to pollution as a result of a relatively short larval stage, which is particularly vulnerable to hostile environments, and their prolongation of adult life span.

In contrast to species richness, species diversity did not reveal clear trends along the pollution gradient, and the McIntosh index reached the second highest value on one of the most contaminated sites (site 2). Within communities, species diversity may increase in several ways. The main mechanism is through an increased range of available resources, which does not seem probable at the most contaminated sites. However, all indices of species diversity are highly sensitive to the presence of dominant species, resulting in high index values for communities with more even species distribution (Clements and Newman 2002). Thus, if some dominant species are eliminated from a community or their population densities decrease due to pollution, the net result is increased species evenness and higher diversity index values at polluted environments.

Carabid species differ in their competitive abilities along environmental gradients. In a model presented by Wisheu (1998), species share a common preference for the same segment of the environmental gradient. Intolerant, competitive

and dominant species occupy the preferred segment of the environmental gradient while tolerant, subordinate species inhabit regions with suboptimal levels of resources. However, competition among insects and other small invertebrates from temperate regions is very weak, because of their small size and intermediate position in a trophic chain (Hanski 1982, Connel 1983, Schoener 1986). Competition among carabid beetles may occur only among dominant species (Loreau 1990, 1993). High scores of the dominant species from locality 5, presented in table 6, indicate that they are good competitors, occupying a preferred segment of the environment. Despite such competition, many species may coexist because of a greater range of available resources at the reference site. A sigmoidal pattern of relative abundance curve (fig 4e) is characteristic for mature communities with a high spectrum of available resources (May 1975, Morris & Lakhani 1979, Morris & Rispin 1987, Ugland & Gray 1982). On site 4, characterized by moderate pollution, the situation is drastically different. All moisture preferring species, which played dominant roles in the community of the reference site, do not occur at site 4. There is, however, one species with high value of niche overlap: *C. violaceus*. Reduction of available resources (food) probably makes the competition stronger, which in turn results in reduction of the abundance of most species. Another dominant species, *C. arvensis*, is placed in a cluster that excludes *C. violaceus*, suggesting different environmental preferences in space and time. The observed reduction of population abundance of *C. violaceus* on site 2 makes it easier for *C. arvensis* to occupy the preferred segment of the environment. In that case, as seen on fig. 4, a higher score of diversity reflects only species evenness, whereas richness is low. It is remarkable that the lack of competitors does not create new space for colonization by other species. In our opinion, the lack of food supplies at the most contaminated sites allows only a few species to survive from the regional pool. This situation is in contrast with data presented by Connel (1978). However, the period of time when disturbance appears in the Connel's model is rather short, while our studies consider

a region chronically polluted over several generations. In the Connell's model, there is enough time to restore all available resources after a disturbance. In contrast, in areas polluted with metals, the disturbance is permanent, limiting the occurrence of most species.

CONCLUSIONS

1. Species richness of ground beetle communities decreased along a metal pollution gradient. However, no clear trend was found for species diversity. This may be the result of a population decrease or elimination of the dominant species and more even species distribution at the contaminated sites.
2. Along the gradient of metal pollution, environmental conditions for soil and epigeic animals change due to accumulation of organic matter at the polluted sites. This situation makes it difficult to distinguish direct toxic effects from indirect influences on carabid communities.
3. Lifecycle variability among carabid species seems to be a very important feature, responsible for differences between species in their responses to metal contamination.

ACKNOWLEDGEMENTS

The authors wish to thank Maria Niklińska and Maciej Maryański for their invaluable help in field and laboratory work. The study was supported by the Polish State Committee for Scientific Research, grant no. KBN-6-P04F-043-18.

REFERENCES

- Berg B., Ekbohm G., Soderstrom B., Staaf H. 1991. Reduction of decomposition rates of Scots pine needle litter due to heavy-metal pollution. *Water Air Soil Pollut.*, 59: 165-177.
- Butovsky R. O. 1997. Heavy metals in invertebrate communities of polluted terrestrial ecosystems in Russia and Western Europe. In: Butovsky R. O. Straalen N. M. van Pollution-induced changes in soil invertebrate food-webs. pp.87-97, Amsterdam and Moscow.
- Chabane K., Josens G., Loreau M. 1994. Laboratory measurement of consumption and growth in *Abax ater*. In: Desender K., Dufrene, M. Loreau M., Luff M. L. & Maelfait, J. -P. (eds.), *Carabid Beetles: Ecology and Evolution*, 109-117, Kluwer Academic Publishers, Dordrecht.
- Clements W., Newman, M.C. 2002. *Community ecotoxicology*. John Wiley & Sons Ltd, Chichester, 336 pp.
- Connell J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Plants and animals. Amer. Nat.*, 122 : 661-696.
- Connell J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199 (4335): 1302-1310.
- Coughtrey P.J., Jones C.H., Martin M.H., Shales S.W. 1979. Litter accumulation in woodlands contaminated by Pb, Zn, Cd and Cu. *Oecologia (Berlin)*, 39: 51-60.
- Desender K., Dufrene M., Maelfait J.-P. 1994. Long term dynamics of carabid beetles in Belgium: a preliminary analysis on the influence of changing climate and land use by means of a database covering more than a century. In: Desender, K., Dufrene, M. Loreau M., Luff, M.L. & Maelfait, J.-P. (eds.), *Carabid Beetles: Ecology and Evolution*, Kluwer Academic Publishers, Dordrecht.
- Dritchilo W., Ervin T.L. 1982. Responses in an abundance and diversity of cornfield carabid communities to differences in farm practices. *Ecology*, 63: 900-904.

- Duelli P., Obrist M., Schmatz D.R. 1999. Biodiversity evaluation in agricultural landscapes: above ground insects. *Agricultures Ecosystems & Environment*. 74: 33 – 64.
- Eyre M.D. 1994. Strategic explanations of carabid species distribution in northern England. In: Desender, K., Duffrène, M. Loreau, M., Luff, M.L. & Maelfait, J.-P. (eds.), *Carabid Beetles: Ecology and Evolution*, 277-281, Kluwer Academic Publishers, Dordrecht.
- Eyre M.D., Lott D.A., Garside A. 1996. Assessing the potential for environmental monitoring using ground beetles (Coleoptera, Carabidae) with riverside and Scottish data. *Ann. Zool. Fennici* 33: 157-163.
- Freitag R., Hastings L., Mercer W.R., Smith A. 1973. Ground beetle populations near a kreft mill. *Canadian Entomologist* 105: 299-310.
- Gongalskii K.B., Butovsky, R.O. 1997. Heavy metal pollution and carabid beetles (Coleoptera, Carabidae) in the vicinity of the Kosogorski metallurgic plant at Kosaya Gora. In: Butovsky, R.O. & Straalen, N.M. van *Pollution-induced changes in soil invertebrate food-webs*. pp. 55-61, Amsterdam and Moscow.
- Greenslad P.J.M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology*, 33: 301-310.
- Grodziński W., Greszta J., Laskowski R., Maryański M., Roýen A. 1990. Effect of the chemical composition of industrial dusts on forest floor organic matter accumulation. *Water Air Soil Pollut.*, 53: 169-178.
- Grüm J. 1975. Mortality patterns in carabid populations. *Ekol. Pol.* 23: 649-665.
- Hakoyama H., Iwasa Y., Nakanishi J. 2000. Comparing Risk Factors for Population Extinction. *J. Theor. Biol.* 204: 327-336.
- Hanski I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Species abundance plants and/or animals. Oikos*. 38: 210-221.
- Hengeveld R. 1980a. Qualitative and quantitative aspects of the food of ground beetles (Coleoptera, Carabidae): a review. *Netherlands Journal of Zoology*, 30: 555-563.
- Hengeveld R. 1980b. Polyphagy, oligophagy and food specialisation in ground beetles (Coleoptera, Carabidae). *Netherlands Journal of Zoology*, 30: 564-584.
- Hengeveld R. 1980c. Food specialisation in ground beetles: an ecological or a phylogenetic process? (Coleoptera, Carabidae). *Netherlands Journal of Zoology*, 30: 585-594.
- Honek A. 1997 a. The effect of plant cover and weather on the activity of ground surface arthropods in a fallow field. *Entomological Research in Organic Agriculture* pp. 203-210.
- Honek A. 1997 b. The effect of temperature on activity of Carabidae (Coleoptera) in a fallow field. *Eur. J. Entomol.* 94: 97-104.
- Hopkin S.P., Martin M.H. 1984. Assimilation of zinc, cadmium, lead and copper by centipede (*Lithobius variegatus* (Chilopoda)). *J. Appl. Ecol.* 21: 535-543.
- Kramarz P. 2000. Cadmium and zinc accumulation and its demographic effects in invertebrates. In: Kammenga J. and Laskowski R. (eds.) *Demography in Ecotoxicology*, John Wiley & Sons: 91-108.
- Laskowski R., Hopkin S.P. 1996. Accumulation of Zn, Cu, Pb and Cd in the garden snail (*Helix aspersa*): implications for predators. *Environmental Pollution* 91: 289-297.
- Loreau M. 1990. Competition in a carabid beetles community: a field experiment. *Oikos* 58: 25-38.

- Loreau M. 1992. Species abundance patterns and the structure of ground beetle communities. *Annales Zoologici Fennici* 28: 49-56.
- Luff M.L. 1975. Some features influencing the efficiency of pitfall traps. *Oecologia*, Berlin, 19: 345-357.
- Magurran A.E. 1988. Ecological diversity and its measurements. Croom Helm Ltd, London, Sydney, pp. 1-179.
- May R.M. 1975. Patterns of species abundance and diversity. In Cody, L. & Diamond, J. M. (eds), *Ecology and evolution of communities*, pp: 81-120. Harvard University Press, Cambridge, Mass.
- Morris M.G., Rispin W.E. 1988. A beetle fauna of oolitic limestone grassland and the response of species to conservation management by different cutting regimes. *Biological Conservation*, 43: 87-105.
- Morris M.G., Lakhani K.H. 1979. Responses of grassland invertebrates to management by cutting. I. Species diversity of Hemiptera. *Journal of Applied Ecology*, 16: 77-98.
- Mozdzer T., Kramarz P., Piúkiewicz A., Niklińska M. 2001. Accumulation of cadmium and zinc in the larval stage of the ground beetle, *Pterostichus oblongopunctatus* F. In: *Abstracts of the SECOTOX World Congress: Ecotoxicology and Environmental Safety on the Verge of Third Millennium: Trends, Threats and Challenges*, Kraków, Poland, 20-24 August 2001.
- Niklińska M., Laskowski R., Maryński M. 1998. Effect of heavy metals and storage time on two types of forest litter: Basal respiration rate and exchangeable metals. *Ecotox. Environ. Safety*, 41: 8-18.
- Pianka E.R. 1974. Niche overlap and diffuse competition. *Proc. nat. Acad. Sci.(Wash.)*, 71: 2141-2145.
- Rayms-Keller A, Olson K.E., McGaw M., Oray C., Carlson J.O., Beaty, B.J. 1998. Effect of heavy metals on *Aedes aegypti* (Diptera: Culicidae) larvae. *Ecotoxicol. Environ. Saf.* 39: 41-47.
- Read H.J., Wheeler C.P., Martin, M.H. 1987. Aspects of the ecology of Carabidae (Coleoptera) from woodlands polluted by heavy metals. *Environmental pollution*. 48: 61-76.
- Schoener T.W. 1983. Field experiment on interspecific competition. *Amer. Nat.* 122: 240-285.
- Sousa W.P. 1984. The role of disturbances in natural communities. *Annu. Rev. Ecol. Syst.* 15: 359-367.
- Strojan C.L. 1978. The impact of zinc smelter emission on forest litter. *Oikos*, 31: 41-46.
- Szafer W., Zarzycki K. 1972. *Szara roślinna Polski*. Tom II, PWN, Warszawa.
- Thiele H.U. 1977. *Carabid Beetles in Their Environments*. Springer -Verlag, Berlin.
- Thomas C.F.G., Parkinson L., Marshall E.J.P. 1998. Isolating the components of active-density for the carabid beetle *Pterostichus melanarius* in farmland. *Oecologia* 116: 103-112.
- Ugland K., Gray J. 1982. Lognormal distribution and concept of community equilibrium. *Oikos* 39: 171-178.
- Walin H., Chiverton P.A., Ekblom B.S., Borg A. 1992. Diet, fecundity and egg size in some polyphagous predatory carabid beetles. *Entomologia experimentalis et applicata*, 65: 129-140.
- Wisheu I.C. 1998. How organisms partition habitats: different types of community organisation can produce identical patterns. *Oikos* 83: 246-258.